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II.

CONTRIBUTIONS FROM THE CRYPTOGAMIC LABORATORY OF HARVARD UNIVERSITY.

XIX. — ON THE DEVELOPMENT OF THE SPERMOGONIUM OF CÆOMA NITENS (SCHW.).

By HERBERT MAULE RICHARDS.

Presented by W. G. Farlow, January 11, 1893.

WHILE the mature condition of the spermogonium of *Cœoma nitens* has been described and figured in more than one instance, there has been little written about its development. The general impression seems to have been that the hyphæ of the fungus, which ramify through the tissues of the leaf, penetrate the walls of the epidermal cells when spermogonia are about to be produced, and that by subsequent growth the spermogonia are formed in the cavities of the epidermal cells so penetrated.* It is exactly this question as to whether the spermogonium actually arises within, and not perhaps between, the epidermal cells, that is the subject of the following remarks. It is more than a year since Professor Farlow suggested to me the advisability of settling this disputed point, but until the present spring I did not have a chance of carrying out the suggestion. In the spring of 1891 I collected in the vicinity of Cambridge a considerable amount of material of the spermogonia of *Cœoma nitens* on *Rubus villosus*. It was gathered in the latter part of April, and was at that time in very young condition, having scarcely begun to show itself on the surface of the leaves. The material was killed in hot picric acid, and was then successively treated with the usual grades of alcohol, so that it was in good condition for examination. At first, free hand sections were wholly used, but afterwards sections cut in paraffin with a microtome were also employed for confirming certain points that could only be settled by serial sections.

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* Burrill, in "The Prairie Farmer," Vol. LVII. p. 762, 1885.

It will be well before speaking of the spermogonia themselves to give a brief description of the hyphæ of the fungus as they appear in the host plant. Before the spermogonia have begun to develop, a section of the affected leaf of the Rubus shows the presence of hyphæ, which ramify through its tissues, without, however, producing any very great distortion in the cells. The hyphæ are of a pretty uniform diameter, and, while at first almost simple, later become considerably branched. They do not seem to traverse the cells themselves to any great extent, if at all, making their way rather between adjacent cells and in the air spaces of the leaf. They do, however, send into the cells curious haustoria which present a very characteristic appearance (Figs. 5 and 9) already figured by Newcomb and Galloway.* At the places where these processes pass through the cell walls they are contracted to a very much smaller diameter than the ordinary hyphæ, but inside the cavity of the cell they become very much expanded, and often curiously knotted. A few characteristic forms have been figured (Fig. 9, *a*, *b*, *c*). The haustoria were more noticeable in the material which had been collected later in the season than in that gathered before the spermogonia were to be seen.

In the region immediately below the epidermis, the hyphæ are very much more thickly massed than in other portions of the leaf, having forced their way in between the epidermal cells and the parenchyma beneath. In this locality, and also to some extent elsewhere, it may be demonstrated by proper staining that the hyphæ are septate, especially after the formation of the spermogonia. In fresh material the contents of the hyphæ are largely hyaline, only occasionally showing a finely granular appearance, and many vacuoles are to be seen. As has already been said, the hyphæ themselves do not excite any marked morbid growth in the tissues of the leaf, but in the immediate neighborhood of the spermogonia there is a very considerable distortion. In leaves that are at all badly affected by the fungus, the chlorophyll very generally changes its color, becoming yellowish or brownish, so that the infected portions are very noticeable on the growing plant. In such cases the whole contents of the epidermal cells, as well as the chlorophyll grains, have disintegrated more or less, particularly in the immediate neighborhood of the spermogonia.

The first indication of the formation of a spermogonium is seen in the activity of the hyphæ which lie immediately below the epidermis. Certain of these hyphæ are seen to send out processes which grow out towards the surface of the leaf. These outgrowths push their way between the epidermal cells, but do not at this early stage enter them, soon becoming, however, multicellular by the formation of frequent cross septa (Figs. 1, 2). At first the cells which surround the developing spermogonium are but little affected, the rapidly growing hyphæ merely splitting the wall at the middle lamella. The space between the cell walls, thus separated and forced apart, affords a cavity in which the hyphæ may grow. The hyphal threads now increase very rapidly in number, both by division and by the sending up of new outgrowths from the hyphæ beneath, so that the parted walls of the adjoining epidermal cells are very much pushed outwards to make room for the developing spermogonium (Fig. 3). At the same time, these hyphæ, which were at first very irregularly arranged, show a tendency to place themselves in parallel rows, and their contents begin to assume a more granular appearance than those of the ordinary vegetative hyphæ. Both of these conditions become more marked as the spermogonium matures.

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* Journal of Mycology, Vol. VI. p. 106, Pl. VI., 1891.

As the spermogonium continues to increase in size, it exerts more and more pressure on the walls of the cells which confine it, and having distended them outwards as far as possible finally ruptures them (Fig. 4, *a*). The rupture takes place from the atrophy of the walls, which have by this time become very much weakened by pressure. The hyphæ are now free to grow into, and eventually fill, the larger space afforded by the union of the cavities of the surrounding cells. The remnants of the ruptured walls are apparently soon absorbed or hidden by the growing hyphæ, for in stages of the spermogonium not a great deal more advanced than this they are very hard to distinguish. It is usually a long time, however, before all traces of the separating wall are lost, as will be noticed in Figure 4, *b*, for even in this much later stage indications of the wall may still be seen in a slight protuberance, which extends downwards into the cavity of the spermogonium. The time in the development of the spermogonium at which the rupture takes place is not at all constant; in some cases where the mass of hyphæ was very small, it was seen to have already broken through the walls. After the hyphæ have made their way into the larger cavity, their parallel arrangement becomes more conspicuous than before, and as the hyphæ continue to multiply in number and increase in size a morbid growth starts up in the cells surrounding them. The cavity in which the spermogonium is forming enlarges very much as the hyphæ continue to grow and fill it. This enlargement takes place chiefly in a vertical direction, although there is a considerable lateral expansion as well, as the spermogonium rises above the surrounding epidermis. The shape finally assumed is that of an inverted truncated cone, but at times the spermogonia are almost pyriform. No differentiation of the hyphæ into anything like a peridium is seen, the cell walls of the host plant remaining as the only covering that the spermogonium has even to maturity. Eventually the upper wall disappears, being apparently absorbed and finally broken through by the hyphæ beneath, which are thus exposed to the air. The abnormal growth that affects the cells in which the spermogonium is developing is also taken up by the epidermal cells which immediately surround it. These increase somewhat in diameter, but chiefly extend themselves in height, and, owing to the excessive development of the top of the spermogonium, are often somewhat bent upon themselves. On one side they cling fast to the spermogonium wall, on the other they are rounded off, rising considerably above the other epidermal cells (Figs. 5, 6). These cells serve the purpose of supporting the spermogonium, the ring of them completely surrounding it, as is shown in the figure of the transverse horizontal section (Fig. 7). Usually a second row of cells, outside of the supporting cells, are also modified to some extent, and serve in turn to support the inner row. In some cases it was observed that a third row of cells was also somewhat distorted, and in leaves which were very thickly beset with spermogonia scarcely an epidermal cell was not to some extent swollen.

The further development of the spermogonium is not of especial interest in this connection. As it matures, it gradually takes on the characteristic orange color of these organs, and the hyphæ are seen to become slightly swollen at the tips. From the tips of the hyphæ the spermatia are abstricted, to be finally liberated by the breaking away of the enveloping cell wall (Fig. 8). It is not infrequently the case that a large number of spermatia are formed before being set free (Fig. 5). The color of the spermogonium is due, as in other Uredineæ, to the bright orange oil-like particles which are found in the hyphæ. In addition to the oil globules, the hyphæ are filled with finely granular matter which also has an orange tinge. The contents of the surrounding epidermal cells are greatly altered, varying from an orange to a brownish yellow color, depending upon their proximity to the spermogonia, and in cases where many spermogonia have developed on a leaf the whole organ takes on a yellowish color.

From the observations described above, it seems impossible to consider the cavity in which the spermogonium develops as originating from a single cell, being rather from the junction of several cells. In other words, the spermogonium starts in the first place as an outgrowth *between*, and not *in*, the epidermal cells of the host, soon however by pressure breaking through and absorbing the confining walls, and making its way into the cavities of the surrounding cells. As the absorption of these walls may take place very early in the development of the spermogonium, before the mass of hyphæ has reached any considerable size, one might be easily deceived into thinking that the spermogonium was forming in the cavity of a single epidermal cell, which had been, perhaps, enlarged somewhat by a morbid growth excited by the fungus. It is also possible that one of the haustoria, already referred to, might have been mistaken for the very earliest stage in the growth of a spermogonium. The question might arise as to whether the young stages herein described were not in reality tangential sections of much older ones, but in the light of the evidence afforded both by the sequence of stages observed and by carefully cut series of sections it is sufficient to say that such could not have been the case.

As regards comparison with other spermogonia, a few words may be of interest. The spermogonium of *Cæoma nitens* is not, it is true, exactly comparable with the typical flask-shaped form usually found in connection with other Uredineæ, as it is much more superficial, the growth starting immediately beneath the epidermis and extending outwards towards the surface of the leaf, while in the case of the spermogonium of *Æcidium berberidis*, for instance, the spermogonium originates in the parenchyma of the leaf, and remains very largely buried in it even to maturity. On the other hand; the spermogonium of which the form found on Anemone is a type is seen to be even more superficial than that of *Cæoma nitens*, the very much flattened cone-shaped masses being located immediately below the cuticula. The course of the development as well as the ultimate result is simpler in *Cæoma nitens* than in *Æcidium berberidis*, as the hyphæ merely remain in parallel rows, and have for their only covering the cell walls of the host plant, while in the case of the flask-shaped spermogonium there is a definite false peridium formed by a more or less distinct matting together of the peripheral hyphæ.

In the former case apparently all of the hyphæ bear spermatia, in the latter case only those in the interior of the flask-shaped mass are fertile. The hyphal portion of the spermogonium of *Cœoma nitens* corresponds then most nearly to the central part of such a spermogonium as is seen in the case of *Æcidium berberidis*.

In the above work a very convenient and satisfactory stain was found in methylene blue. This was used in a one per cent solution, and the sections were stained on the slide. The sections were first considerably overstained, and then, by treatment with acetic acid, were decolorized to just the point desired. The process of decolorization was watched under the microscope and stopped when enough of the stain had been washed out. The acetic acid having been thoroughly gotten rid of, the sections were then mounted in glycerine according to the usual method. By means of this decolorization some differentiation in the staining was brought out, for the acid has a tendency to extract the color from the cells of the host more quickly than from the hyphæ of the parasite, so that in a section of the leaf the latter show out much more plainly than they would otherwise have done. In the case of sections cut in paraffin the acetic acid also served to swell up the somewhat shrunken tissues to a more natural appearance.

EXPLANATION OF FIGURES.

Fig. 1. A very early stage of the spermogonium.
" 2. A slightly more advanced condition, but before the hyphæ have any definite arrangement.
" 3. Showing the splitting apart of the walls of the epidermal cells, and also the parallel arrangement of the hyphæ in the young spermogonium.
" 4. *a*, showing the rupture of the walls by the hyphæ. *b*, a more advanced stage, where there is only a trace of the dividing wall left.
" 5. A mature spermogonium with only one row of supporting cells.
" 6. A mature spermogonium with the normal two rows of supporting cells.
" 7. Horizontal section of mature spermogonium.
" 8. Hyphæ from spermogonium showing formation of spermatia.
" 9. *a, b, c.* Haustoria.

Figures 1 to 7 × 425 diameters; Figures 7 and 8 × 650 diameters. Figures 1 to 4 drawn from sections of alcoholic material; Figures 5 to 9, from fresh specimens. All figures drawn with Abbe camera.

June, 1892.

Richards-Cæoma Nitens.